A REVIEW OF RECENT AND QUATERNARY ORGANIC-WALLED DINOFLAGELLATE CYSTS OF THE GENUS *PROTOPERIDINIUM*

by REX HARLAND

ABSTRACT. A review is given of Recent and Quaternary organic-walled dinoflagellate cysts belonging to the genus *Protoperidinium* Bergh emend. Balech 1974. There is a similarity between the taxonomies based upon thecal and cyst morphologies, the major difference being one of hierarchy. A scheme is presented which attempts to amalgamate the two taxonomic systems, and which shows the range of cyst morphology attributable to a single living genus, the general non-conservative nature of certain cyst morphologies, and the use of common cyst forms amongst different dinoflagellates. Two new names, *Fuscusasphaeridium* and *Asymmetropedinium*, are introduced, and *Quinquecuspis* Harland is emended and diagnosed in Latin.

RECENTLY a number of important reviews have appeared describing the taxonomy of peridiniacean dinoflagellates and their cysts. These include Lentin and Williams (1975) and Stover and Evitt (1978), both of which were mainly concerned with dinoflagellate cysts, their morphology, and particularly their archeopyle shape and structure. Unfortunately little or no attention was paid to the taxonomy of extant dinoflagellates and their cysts, or to the recently fossilized cysts found in Quaternary sediments. Similarly, in the field of phycology a major revision of a part of the genus *Peridinium* Ehrenberg 1832 was published by Balech (1974), but with little reference to dinoflagellate cysts. This paper attempts to look at the classification of living peridiniacean dinoflagellates, particularly those associated with the genus *Peridinium*, in relation to Recent and Quaternary dinoflagellate cysts.

TAXONOMY OF THE GENUS *PERIDINIUM*

The genus *Peridinium* was erected in 1832 by Ehrenberg with *Peridinium cinctum* (O. F. Müller) as the type species. In the early part of the twentieth century, with the advent of major oceanographical expeditions and the increasing number of species attributed to the genus (now well over 200) a number of schemes to subdivide the genus were published. Jörgensen (1913) comprehensively reclassified the genus, and used the number of plates that border the first apical as the principal character in the formation of subgenera, and the pattern of the dorsal plates on the epitheca, in particular the relationship with the precingular plate series, for the division of the subgenera into sections.

In the first instance the genus was divided into two subgenera: *Orthoperidinium* [1′ contacts four plates 1″, 2′, 4′, and 7″] and *Metaperidinium* [1′ contacts five plates 2′, 1″, 2″, 4′, and 7″]. The third condition *Paraperidinium* [1′ contacts six plates 2′, 1″, 2″, 4′, 6″, and 7″] was not given subgeneric status because of the considerable variation in the length of the sutures between the plates. The subgenus *Orthoperidinium* was then divided into the following three sections:

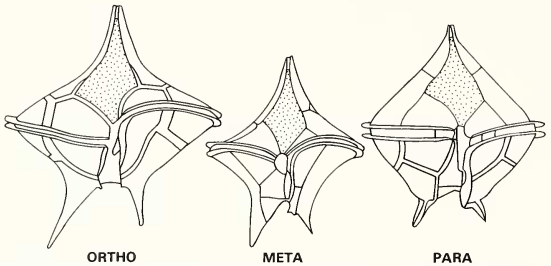
Tabulata	2a plate contacts 3″ and 4″ or 4″ and 5″ plates
Conica	2a plate contacts 3″, 4″, and 5″
Oceanica	2a plate contacts 4″ only,

Similarly the subgenus *Metaperidinium*:

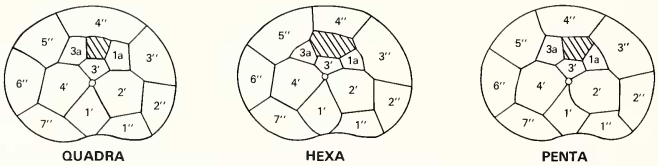
Pyriformia	2a plate contacts 3″ and 4″ or 4″ and 5″
Paraperidinium	see discussion above
Humilia	2a plate contacts 4″ only; with solid antapical horns
Divergens	as above with hollow antapical horns.

[Palaeontology, Vol. 25, Part 2, 1982, pp. 369–397, pls. 38–42.]

This system was revised by Paulsen (1931) to take into account a greater number of characters, and he used the terms 'ortho'-contacts 1″, 2′, 3′, 4′, and 7″, 'meta'-contacts 1″, ± 2″, 2′, 3′, 4′, ± 6″, and 7″, and 'para'-contacts 1″, 2″, 2′, 3′, 4′, 6″, and 7″ to characterize the first apical plate (see text-fig. 1); and 'quadra'-contacts 4″ only, 'hexa'-contacts 3″, 4″, and 5″ and 'penta'-contacts 3″ and 4″ to characterize the dorsal epithecal configuration, especially the contacts at the posterior border (see text-fig. 2). Paulsen included in his treatment of *Peridinium*, forms with two intercalary plates as



TEXT-FIG. 1. Species of *Protoperidinium* illustrating the three different types of first apical plates (after Graham 1942). The first apical plate is stippled. The ortho species also shows growth bands.



TEXT-FIG. 2. Examples of the three different styles of dorsal epithecal tabulation (after Graham 1942). The second dorsal intercalary plate is hachured.

opposed to the normal three referring them to the subgenus *Archaeperidinium* (=genus *Archaeoperidinium* of Jörgensen (1913)). These taxonomic schemes all rely upon the 'stability' of plate patterns in the region of the first apical and dorsal epithecal plates and in general on the possession of three dorsal intercalary plates. Graham (1942) noted, however, that the number of plates in the cingulum could be important in the taxonomy of *Peridinium* species and that their study had been neglected despite the fact that the dissection of the plates was not difficult.

Balech (1974), in his major revision of a part of the genus *Peridinium*, used the nature of the cingular plates to differentiate between freshwater *Peridinium sensu stricto* with five cingular plates, and marine *Peridinium* species with four cingular plates. The generic name *Protoperidinium* Bergh was used to accommodate these marine species. *Protoperidinium* was then subdivided into three subgenera based upon the number of precingular and intercalary plates. Further subdivisions were recognized using the criteria first employed by Jörgensen (1913) and Paulsen (1931).

Although the basis of this taxonomic subdivision is the number, shape, and size of the plates together with the tabulation pattern, I have never seen a reasoned account explaining why the number of cingular plates and the number of intercalary plates should be given hierarchical priority over the configuration of the first apical plate, or why the configuration of the first apical plate should be given

priority over the mutual relationship of the second intercalary plate and its neighbours. Indeed, evidence from the cyst morphology suggests that the shape and relative position of the second intercalary plate is possibly *more* significant, because it is through this site that excystment occurs. Recent work by Gocht and Netzel (1974, 1976) on the overlap system in peridiniacean and gonyaulacacean dinoflagellates (Dürr and Netzel 1974) has suggested that this second intercalary site is the keystone for both overlap or imbrication (Dörhöfer and Davies 1980), and in archeopyle formation, and that it must be genetically determined. This is in contrast to the first apical plate which does not appear to play such a major role in thecal or cyst function.

It is, however, Balech's (1974) scheme that is used herein as a basis for discussing the contribution of cyst morphology. We are obliged to use thecal morphology as the starting-point since the information is potentially complete and only a small proportion of the dinoflagellates produce fossilizable cysts as a part of their life-cycle (Dale 1976). Cysts of the genus *Protoperidinium* are known to have a varied morphology ranging from simple spheres to quite complex cysts with processes and horns. Often the common unifying feature is the style of archeopyle formation, which always involves the use of an intercalary paraplate with or without its adjacent paraplates. Only in rare cases is it possible to distinguish a clear paratabulation. In this study emphasis is necessarily placed upon gross morphology and archeopyle formation in investigating the relationships of the various *Protoperidinium* cysts to their respective thecal stages.

SYSTEMATIC DESCRIPTIONS

In each of the subsequent discussions of genera, subgenera, sections, and species, the relevant cyst morphologies will be particularly noted, with further comment reserved for later sections. Cysts known to the author are described in some detail, otherwise the reader is referred to the best published description. The accompanying thecal tabulation diagrams have been standardized, do not necessarily correspond to details of the particular taxa in nature, and should therefore be treated as diagrammatic.

All the cysts illustrated here are registered in the MPK series and are housed in the Palynological Collections of the Institute of Geological Sciences (IGS), Leeds.

The taxonomic changes that have resulted from this review, including the erection of two new taxa and the change in status of several others, are all handled within the Appendix. The taxonomic system used herein is, however, summarized in Table 1.

Division PYRRHOPHYTA Pascher 1914
Class DINOPHYCEAE Fritsch 1929
Order PERIDINIALES Haeckel 1894
Family PERIDINIACEAE Ehrenberg 1832
Genus PROTOPERIDINIUM Bergh *emend* Balech 1974

Type species. Protoperidinium pellucidum Bergh 1881; S.D. by Loeblich, Jr. and Loeblich, III, 1966.

Remarks. This genus accommodates, for the most part, the marine species formerly belonging to the genus *Peridinium* Ehrenberg. They have four cingular plates in contrast to the five in *Peridinium sensu stricto*. An exception is *P. faeroense* Paulsen which has five cingular plates (Dale 1978). The type species possesses a para first apical plate arrangement and a hexa dorsal epithecal configuration (text-fig. 3). Cysts capable of fossilization have not been recorded for the type species.

Subgenus *Minusculum* (Lebour) Balech 1974

Type species. Protoperidinium (*Minusculum*) *bipes* (Paulsen) Balech 1974; O.D.

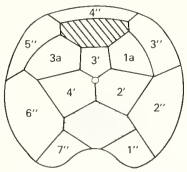
Remarks. This subgenus is characterized by six precingular plates and three intercalary plates. The unique 'boomerang' shape of plate 6″ (Balech 1974) is also a significant feature (text-fig. 4). No fossilizable cysts have been observed from species attributable to this subgenus.

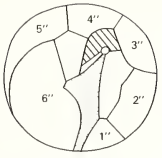
TABLE 1. Taxonomy of *Protoperidinium* species that produce fossilizable cysts

GENUS	SUBGENUS			SECTION	SPECIES
Protoperidinium	*Minusculum*			—	—
	Archaeperidinium			*Archaeperidinium* stat. nov.	*minutum*
				Stelladinium stat. nov.	*compressum*
				Fuscusasphaeridium nomen nov.	*avellana* *denticulatum* *excentricum*
	Protoperidinium	Para	Quadra		—
			Penta		—
			Hexa	*Protoperidinium* stat. nov.	*latissimum*
		Meta	Quadra	—	—
			Penta	—	—
			Hexa	—	—
		Ortho	Quadra	*Votadinium* stat. nov.	*claudicans* *oblongum*
			Penta	*Asymmetropedinium* nomen nov.	*punctulatum*
			Hexa	*Brigantedinium* stat. nov.	*conicoides*
				Selenopemphix stat. nov.	*conicum* *nudum* *subinerme*
				Quinquecuspis stat. nov.	*leonis*
				Trinovantedinium stat. nov.	*pentagonum*

TABLE 1. Taxonomy of *Protoperidinium* species that produce fossilizable cysts

GENUS	SUBGENUS			SECTION	SPECIES
Protoperidinium	*Minusculum*			—	—
	Archaeperidinium			*Archaeperidinium* stat. nov.	*minutum*
				Stelladinium stat. nov.	*compressum*
				Fuscusasphaeridium nomen nov.	*avellana* *denticulatum* *excentricum*
	Protoperidinium	Para	Quadra		—
			Penta		—
			Hexa	*Protoperidinium* stat. nov.	*latissimum*
		Meta	Quadra	—	—
			Penta	—	—
			Hexa	—	—
		Ortho	Quadra	*Votadinium* stat. nov.	*claudicans* *oblongum*
			Penta	*Asymmetropedinium* nomen nov.	*punctulatum*
			Hexa	*Brigantedinium* stat. nov.	*conicoides*
				Selenopemphix stat. nov.	*conicum* *nudum* *subinerme*
				Quinquecuspis stat. nov.	*leonis*
				Trinovantedinium stat. nov.	*pentagonum*





TEXT-FIG. 3 (*left*). Epithecal tabulation of *Protoperidinium* (*Protoperidinium*) *pellucidum* Bergh ex Loeblich, Jr. and Loeblich, III (after Lebour 1925).

TEXT-FIG. 4 (*right*). Epithecal tabulation of *Protoperidinium* (*Minusculum*) *bipes* (Paulsen) Balech (after Balech 1974).

Subgenus *Archaeperidinium* (Jörgensen) Balech 1974

Type species. Protoperidinium (*Archaeperidinium*) *minutum* (Kofoid) Loeblich, III, 1969; O.D.

Remarks. Archaeperidinium has seven precingular plates, an ortho first apical and two intercalary plates, and contains at least five species that are known to produce fossilizable cysts. These are described and discussed herein.

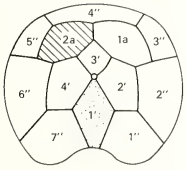
Protoperidinium (*Archaeperidinium*) *minutum* (Kofoid) Loeblich, III 1969

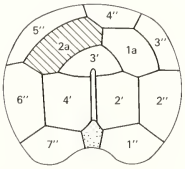
Text-fig. 5

Remarks. The thecal plate configuration of this the type species shows the distinct ortho first apical and two symmetrically placed intercalary plates. The cysts produced by this species are described in Wall and Dale (1968) and illustrated on their pl. 4, fig. 7 but they have not been seen by the present author. The archeopyle, however, is reported to be intercalary (? 1a or 2a) but is rarely seen as an aperture; Wall and Dale's (1968) illustration appears to show an attached operculum. The cyst is otherwise characterized by short, hollow processes with a flat-topped distal extremity that bears spinules around the circumference. The cysts are known from Recent sediments. Incubation experiments (Wall and Dale 1968) have clearly established the link between this theca and cyst.

Protoperidinium (*Archaeperidinium*) *avellana* (Meunier) Balech 1974

Text-fig. 6, 7B; Plate 38, figs. 4–9



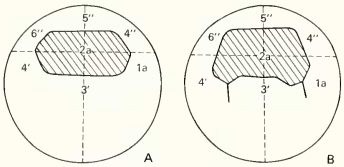


TEXT-FIG. 5 (*left*). Epithecal tabulation of *Protoperidinium* (*Archaeperidinium*) *minutum* (Kofoid) Loeblich, III (after Wall and Dale 1968).

TEXT-FIG. 6 (*right*). Epithecal tabulation of *Protoperidinium* (*Archaeperidinium*) *avellana* (Meunier) Balech (after Wall and Dale 1968).

Remarks. The thecal tabulation illustrated shows the salient features but it is interesting to note that there is some asymmetry in the position of the intercalary plates and especially plate 4″. The cysts of this species have been described and illustrated by Wall and Dale (1968, pl. 4, fig. 2) and consist of spherical, smooth-walled brown bodies with a single dorsal intercalary archeopyle. The shape of the operculum is seen in Wall and Dale (1968), Reid (1977), Harland (1977) and in the present illustrations. The degree of reflection of the detailed thecal plate shape is often quite remarkable.

There can be some confusion between these cysts and those of *P.* (*A.*) *denticulatum* (Gran and Braarud) Balech 1974 although the archeopyles are distinct (text-fig. 7). In palynological preparations many such cysts are often so crumpled that a proper analysis of the archeopyle shape is not always possible. Also, the archeopyle shape can be somewhat modified and need not be a perfect reflection of the thecal plate counterpart. Incubation experiments (Wall and Dale 1968) have established the link between this theca and this cyst.



TEXT-FIG. 7. Apical view of the cysts A—*Protoperidinium* (*Archaeperidinium*) *denticulatum* (Gran and Braarud) Balech (after Wall and Dale 1968), and B—*P.* (*A.*) *avellana* (Meunier) Balech showing the distinct archeopyle shapes, both symmetrical.

The cyst was originally described as *Chytroeisphaeridia cariacoensis* Wall 1965, but may be placed in Reid's (1977) genus *Brigantedinium* recently validated by Harland and Reid (1980) in Harland, Reid, Dobell, and Norris (1980). However, the type species of *Brigantedinium*, *B. simplex*, is the cyst of *P.* (*Protoperidinium*) *conicoides* (Paulsen) Balech, a member of a separate subgenus. The placement of *P.* (*A.*) *avellana* in *Brigantedinium* may, therefore, be inappropriate and perhaps a separate designation needs consideration (see later discussion).

Cyst description. Simple spheroidal brown cyst made up of autophragm or with two very closely adpressed wall layers. Paratabulation not present although the archeopyle shape does hint at the configuration of the 2a, 4′, 3′, and 1a contacts (text-fig. 7B). Cyst wall generally smooth but may appear somewhat shagreenate; the possible indications of two indentations on the ? sulcal area may be a reflection of flagellar pores. Archeopyle intercalary formed by the loss of paraplate 2a which is transversely elongate and symmetrical (see text-fig. 7B). Operculum free. Cyst diameters fall generally within the range 50·0–55·0 μm.

EXPLANATION OF PLATE 38

All figures are illustrated at a magnification of × 500 and were photographed in plain transmitted light unless otherwise indicated.

Figs. 1–3. *Protoperidinium* (*Protoperidinium* sect. *Brigantedinium*) *conicoides* (Paulsen) Balech, Nomarski interference contrast. 1, dorsal view of MPK 1232 showing simple morphology and standard hexa archeopyle. 2, ventral view of MPK 1232 with the two flagellar indentations. 3, dorsal view with the archeopyle and operculum, specimen MPK 1243.

Figs. 4–9. *Protoperidinium* (*Archaeperidinium* sect. *Fuscusasphaeridium*) *avellana* (Meunier) Balech, figs. 4 and 5 by Nomarski interference contrast. 4, apical view showing symmetrical archeopyle with operculum in place, specimen MPK 1236. 5, ditto, specimen MPK 1238. 6, oblique view with operculum coming free, specimen MPK 1235. Figs. 7–9, various levels of focus showing operculum free and more crumpled nature of the cyst, specimen MPK 2768.

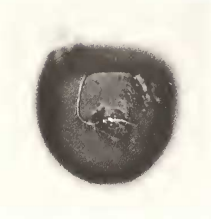
Figs. 10–12. ?Indet. *Protoperidinium* cyst, various levels of focus to show the general morphology and the zigzag archeopyle split, specimen MPK 2769.

1

2

3

4

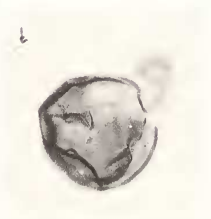


5

6

7

8



9

10

11

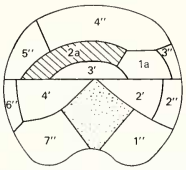
12

HARLAND, *Protoperidinium*

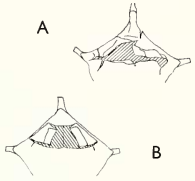
Protoperidinium (*Archaeperidinium*) *compressum* (Abé) Balech 1974

Text-figs. 8, 9; Plate 39, fig. 12

Remarks. The thecal tabulation shows the features of this subgenus, but in particular the asymmetry in the disposition of the intercalary and 4″ plates is worth noting. Text-fig. 8 shows the theca as expanded whereas in life the species is compressed dorso-ventrally, hence the name. The cyst of this species is particularly striking in its stellate morphology, and has been described by Wall and Dale (1968), Bradford (1975), Reid (1977), and Harland (1977). The archeopyle is intercalary and formed by the displacement of two paraplates which remain attached laterally (text-fig. 9). They are



TEXT-FIG. 8 (*left*). Epithecal tabulation of *Protoperidinium* (*Archaeperidinium*) *compressum* (Abé) Balech (after Wall and Dale 1968).



TEXT-FIG. 9 (*right*). Archeopyle formation in *Protoperidinium* (*Archaeperidinium*) *compressum* (Abé) Balech, A—Specimen MPK 1256 (see Pl. 39, fig. 12), B—Idealized scheme.

symmetrically placed and fold back to open a large archeopyle. It is thought that both 1a and 2a paraplates are involved. They do not appear to reflect the asymmetry of the theca. These cysts are unique and to date at least two species (herein Pl. 39, fig. 12, and in Wall and Dale 1968, pl. 2, figs. 15–17) are known, only one of which can be definitely assigned to *P.* (*A.*) *compressum*. Incubation experiments (Wall and Dale 1968) have established the link between this theca and the illustrated cyst described below.

Cyst description. Stellate, peridinioid cysts, compressed dorso-ventrally made up of autophragm. Wall smooth, and epitract smaller than hypotract. Cyst carries one apical, two antapical, and two lateral horns that are long, solid, and acicular. Thickening of the horn bases is sometimes apparent. Paratabulation not present. Archeopyle intercalary formed by the opening of two intercalary paraplates that remain attached laterally. Cysts range in length, excluding the processes, from 26·0–37·0 μm.

Protoperidinium (*Archaeperidinium*) *denticulatum* (Gran and Braarud) Balech 1974

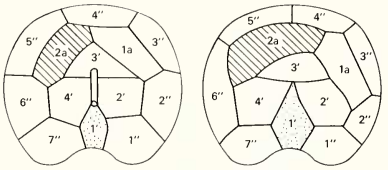
Text-figs. 7A, 10

Remarks. The tabulation of this species shows a remarkable similarity to that of *P.* (*A.*) *avellana* especially with respect to the slight asymmetry of the two intercalary plates; best seen in relation to the position of plate 4″. It is, therefore, perhaps not surprising that the cyst illustrated and described by Wall and Dale (1968, pl. 3 fig. 30) is very similar to that produced by *P.* (*A.*) *avellana* (see Wall and Dale 1968, p. 277) although the identification is admittedly not positive. Archeopyle formation is by loss of a single transversely elongate intercalary paraplate whose configuration is symmetrical, but unlike that of *P.* (*A.*) *avellana* (text-fig. 7). In palynological preparations confusion between the two forms is common. The form illustrated here has a provisional assignment to this species. Incubation experiments by Wall and Dale (1968) failed to positively identify the theca therefore a clearly established link between this theca and cyst is not possible.

Protoperidinium (*Archaeperidinium*) *excentricum* (Paulsen) Balech 1974

Text-fig. 11

Remarks. The thecal tabulation of this species is very similar to both those of *P.* (*A.*) *avellana* and *P.* (*A.*) *denticulatum*. The cysts are brown oval bodies that Wall and Dale (1968, p. 278) describe as being flattened in a polar direction. The archeopyle has not been described. Cysts attributable to this species have not been seen by the present author. Although cysts enclosed by thecae were recorded by Wall and Dale (1968) it is not clear if any thecae were obtained by incubation and positively identified.



TEXT-FIG. 10 (*left*). Epithecal tabulation of *Protoperidinium* (*Archaeperidinium*) *denticulatum* (Gran and Braarud) Balech (after Wall and Dale 1968).

TEXT-FIG. 11 (*right*). Epithecal tabulation of *Protoperidinium* (*Archaeperidinium*) *excentricum* (Paulsen) Balech (after Lebour 1925).

Discussion of the subgenus *Archaeperidinium*

Dinoflagellate cysts of the subgenus *Archaeperidinium* fall into three distinct categories. The first is exemplified by the type species, a cyst with short processes and a single intercalary archeopyle; the second a stellate cyst with a two paraplate intercalary archeopyle; and finally the third with brown spherical/spheroidal cysts with single intercalary transversely elongate archeopyle. These differences in gross cyst morphology underline differences in the tabulation pattern; the type species is symmetrical; the second is very markedly asymmetrical and divided laterally into a clearly marked dorsal and ventral epitheca, and finally those that are only slightly asymmetrical especially in regard to the position of plate 4''. I believe this is a sufficiently natural genotypic division to warrant the application of particular names. The names chosen are derived from both biological and palaeontological literature and include *Stelladinium* Bradford 1975, a name coined to apply to the unique stellate morphology of *P. compressum* cysts. Herein I shall treat them as separate sections such that:

1. *Protoperidinium* (*Archaeperidinium* sect. *Archaeperidinium* stat. nov.) includes *minutum*
2. *Protoperidinium* (*Archaeperidinium* sect. *Stelladinium* stat. nov.) includes *compressum*
3. *Protoperidinium* (*Archaeperidinium* sect. *Fuscusasphaeridium* nomen nov.) includes *avellana*, *denticulatum*, and *excentricum*

The only new name, *Fuscusasphaeridium*, is formally erected in the appendix together with the change of status of the other two taxa. This approach hopefully embodies the general ideas expressed by Wall and Dale (1968), Dale (1976 and 1978), and Reid and Harland (1977). An amalgamation of systems should be possible since we are dealing with common organisms, albeit at different stages of their life-cycle.

Some difficulties are still apparent, for instance *P.* (*P.*) *punctulatum* (Paulsen) also has brown spherical cysts with transversely elongate archeopyles but with a very different thecal tabulation. Possible differences in cyst archeopyle morphology, i.e. ? attached and an asymmetrical opercula (see later discussion) may serve to differentiate them from cysts of *P. punctulatum*.

Subgenus *Protoperidinium* (Bergh) Balech 1974

Type species. Protoperidinium (*Protoperidinium*) *pellucidum* Bergh 1881, S. D. by Loeblich, Jr. and Loeblich, III, 1966.

Remarks. The thecal tabulation of *P.* (*P.*) *pellucidum* has already been discussed, see text-fig. 3. Balech (1974) does, however, subdivide the subgenus into a number of units based upon the pattern of the first apical plate and its adjacent plates, and then again on the dorsal intercalary configuration. Since the type species has a para first apical plate that group will be discussed first.

A. Para-species

i. Quadra. No fossilizable cysts attributable to dinoflagellates in this group are known.

ii. Penta. No fossilizable cysts attributable to dinoflagellates in this group are known.

iii. Hexa. Only one species within this unit is known to produce fossilizable cysts and that is described below. The type species, *P.* (*P.*) *pellucidum*, also belongs in this group.

Protoperidinium (*Protoperidinium*) *latissimum* (Kofoid) Balech 1974

Remarks. The thecal tabulation of this species clearly demonstrates the para first apical plate and the hexa dorsal intercalary arrangement and the symmetry of the pattern. The fossilizable cyst for this species has been described by Wall and Dale (1968) as large, pentagonal, and dorso-ventrally compressed. A paracingulum is represented by broad weakly excavated lateral lobes. The epitract is triangular in outline and large, while the hypotract is much smaller and has two small antapical horns. The archeopyle is intercalary, has a hexa shape but is asymmetrical (*see* Wall and Dale 1968, pl. 2, fig. 7), is large, taking up most of the dorsal surface of the cyst. The operculum is free. Incubation experiments (Wall and Dale 1968) have firmly linked this theca with this cyst.

The cyst genus *Leipokatium* Bradford 1975 was erected to accommodate cysts very similar to that described above. Since, however, the type species for the subgenus also is assigned to this group it might be prudent to suppress *Leipokatium* in favour of *Protoperidinium* (*Protoperidinium* sect.

EXPLANATION OF PLATE 39

All figures are illustrated at a magnification of × 500 and were photographed in plain transmitted light unless otherwise indicated.

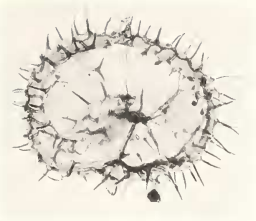
Figs. 1–3. *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *conicum* (Gran) Balech. 1, apical view to show the reniform ambitus and offset standard hexa archeopyle, specimen MPK 2770. 2, ditto, specimen MPK 2771. 3, ditto, specimen MPK 2772.

Figs. 4, 5. Indet. ?*Protoperidinium* cyst, *Xandarodinium xanthum* Reid. 4, ?apical view showing over-all morphology, Nomarski interference contrast, specimen MPK 1261. 5, ditto, specimen MPK 2773.

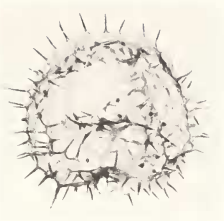
Fig. 6. *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *subinerme* (Paulsen) Loeblich, III, apical view showing broad paracingular zone, lack of ornament, and offset archeopyle with operculum, specimen MPK 1634.

Figs. 7–11. *Protoperidinium* (*Protoperidinium* sect. *Trinovantedinium*) *pentagonum* (Gran) Balech. 7, dorsal view showing the broad hexa archeopyle, hyaline nature of the cyst, and the paracingulum. 8, ventral view with parasulcus and planar paracingulum. 9, optical section illustrating the nature of the apical boss, specimen MPK 1240. 10, dorsal view with broad hexa operculum and nature of the parasutural and intratabular spines. 11, ventral view and deeply indented parasulcus, specimen MPK 2774, all figures with Nomarski interference contrast.

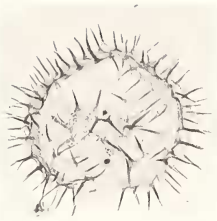
Fig. 12. *Protoperidinium* (*Archaeperidinium* sect. *Stelladinium*) *compressum* (Abé) Balech 1974, dorsal view showing stellate morphology and the 2I archeopyle with the two opercular paraplates attached laterally, Nomarski interference contrast, specimen MPK 1256.



1



2



3

4

5

6

7

8

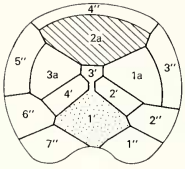
9

10

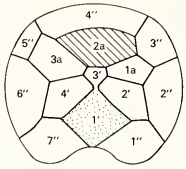
11

12

HARLAND, *Protoperidinium*



TEXT-FIG. 12 (*left*). Epithecal tabulation of *Protoperidinium* (*Protoperidinium*) *latissimum* (Kofoid) Balech (after Wall and Dale 1968).



TEXT-FIG. 13 (*right*). Epithecal tabulation of *Protoperidinium* (*Protoperidinium*) *claudicans* (Paulsen) Balech (after Wall and Dale 1968).

Protoperidinium stat. nov.). However, no fossilizable cysts are known from the type species and therefore the thecal and cyst morphologies cannot be compared. In fact certain thecal tabulation details are different between *P. pellucidum* and *P. latissimum*, but it is difficult to know if these are taxonomically significant at this level (compare text-figs. 3 and 12).

B. Meta-species

Fossilizable cysts have not been described from Modern species attributable to the quadra, penta, or hexa subdivisions of this unit. However, it is of interest that a new species of *Phthanoperidinium* described by Edwards and Bebout (1981) has a meta configuration.

C. Ortho-species

This group contains the most numerous fossilizable *Protoperidinium* cysts and like those above can be subdivided as follows:

i. Quadra. This includes the species *P.* (*P.*) *claudicans* (Paulsen) Balech 1974 and *P.* (*P.*) *oblongum* (Aurivillius) Balech 1974. Balech (1974) considers the latter to be a part of *P.* (*P.*) *oceanicum* Vanhöffen. Both species produce fossilizable cysts.

Protoperidinium (*Protoperidinium*) *claudicans* (Paulsen) Balech 1974

Text-fig. 13

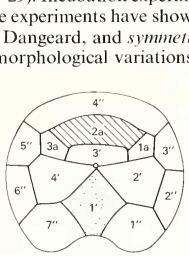
Remarks. The roughly symmetrical thecal tabulation clearly shows the ortho first apical plate and a penta dorsal configuration. This perhaps indicates that the dorsal configuration is subject to some phenotypic variation as this species is usually placed in the quadra group (Balech 1974) although it is admitted that some possess the penta pattern. The cyst of this species has been described by Wall and Dale (1968) and Reid (1977). In dorsal view it is a chordate cyst that bears numerous short-pointed spines. Paratabulation not present but the parasulcus is deep and separates the two broad asymmetrical antapical lobes. Paracingulum not observed. Archeopyle formation is reported to be by loss of the 2a intercalary paraplate which is subapical in position and has a tendency to truncate the apex. Its shape tends to be pentagonal and if indeed only the one paraplate is involved then it is surely an enlarged archeopyle. Incubation experiments have confidently established the theca/cyst relationship in this species (Wall and Dale 1968). These cysts have in the past been included in Reid's (1977) genus *Votadinium*.

Protoperidinium (*Protoperidinium*) *oblongum* (Aurivillius) Balech 1974

Text-fig. 14; Plate 40, figs. 10–12

Remarks. The thecal tabulation as illustrated clearly demonstrates the ortho first apical plate and quadra 2a plate and the symmetrical nature of the over-all pattern. The cyst of this species has been

described by Wall and Dale (1968), Reid (1977), and Harland (1977), with the last two authors referring it to Reid's (1977) genus *Votadinium*. It may be that this species also exhibits variation in the dorsal thecal configuration, as in *P. claudicans*, since there appears to be some variation in cyst morphology (see Wall and Dale 1968, pl. 1, figs. 23–29). Incubation experiments have established the theca/cyst relationship within the species, but some experiments have shown that relationships exist with the varieties *latidorsale* Dangeard, *inaequale* Dangeard, and *symmetricum* Dangeard and this may in part explain some, if not all, of the cyst morphological variations.



TEXT-FIG. 14. Epithecal tabulation of *Protoperidinium* (*Protoperidinium*) *oblongum* (Aurivillius) Balech (after Wall and Dale 1968).

Cyst description. The cysts are chordate and smooth, formed of autophragm. They possess a clearly defined deeply indented parasulcus which effectively divides the two rounded antapical lobes. Faint traces of probable reflected flagellar pores may sometimes be seen in the sulcus. Paracingulum not seen. The archeopyle is broad and quite large and appears to reach the apex of the cyst on the dorsal surface, giving the cyst a truncated appearance similar to *P. claudicans*. Whether this archeopyle is an enlarged intercalary involving the loss of paraplate 2a or whether it includes paraplates 1a, 2a, 3a, and 3′ is not known. Cyst diameters range from 54·0 to 75·0 μm.

Discussion of ortho quadra *Protoperidinium* species

The two species of this subdivision of the subgenus are clearly related in terms of both their thecal tabulation and cyst morphology. The cysts have in common their over-all chordate morphology and archeopyle style despite the uncertainty as to which paraplates may be involved. The use of a particular name to identify the condition is, therefore, clearly necessary. In this instance *Votadinium* is available for use as a section of the subgenus; hence *Protoperidinium* (*Protoperidinium* sect. *Votadinium* stat. nov.).

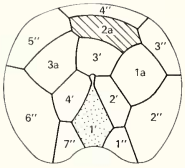
The variation in the dorsal tabulation of *P. claudicans* and the variation in the cysts of *P. oblongum* may point to a deficiency in the taxonomy of these species, with perhaps a lack of sufficient evidence on the varieties that exist and their respective cysts. Further incubation experiments are essential to more closely define the apparent variation.

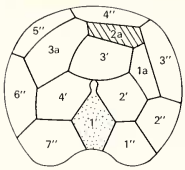
ii. Penta. Only one species *Protoperidinium* (*Protoperidinium*) *punctulatum* (Paulsen) Balech 1974 produces fossilizable cysts and is included here.

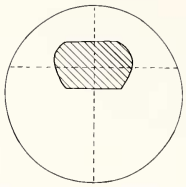
Protoperidinium (*Protoperidinium*) *punctulatum* (Paulsen) Balech 1974

Text-figs. 15–17; Plate 42, figs. 3–6

Remarks. This dinoflagellate, although usually penta, can have a hexa dorsal configuration as seen in the illustrations, and can appear slightly asymmetrical. The cyst has been described by Wall and Dale (1968) and is spherical, brown, with a large intercalary archeopyle formed by the loss of paraplate 2a. Operculum may be attached (Wall and Dale, pl. 2, fig. 27). The aperture is transversely elongate but is asymmetrical and this may be a significant difference compared with the cysts of *P.* (*A.*) *avellana* and *P.* (*A.*) *denticulatum* (compare text-figs. 7 and 17). Confusion between all these cysts can occur if well-preserved, three-dimensional orientated specimens are not available. However, the nature of the archeopyle and thecal tabulation does serve to distinguish this dinoflagellate from other species. Wall and Dale (1968) have established by incubation the link between this theca and cyst.







TEXT-FIG. 15 (*left*). Epithecal tabulation of a hexa *Protoperidinium* (*Protoperidinium*) *punctulatum* (Paulsen) Balech (after Wall and Dale 1968).

TEXT-FIG. 16 (*centre*). Epithecal tabulation of a penta *Protoperidinium* (*Protoperidinium*) *punctulatum* (Paulsen) Balech (after Lebour 1925).

TEXT-FIG. 17 (*right*). Apical view of the cyst of *Protoperidinium* (*Protoperidinium*) *punctulatum* (Paulsen) Balech showing the laterally elongate, asymmetrical archeopyle.

A name is required to accommodate these dinoflagellates and to differentiate them from section *Fuscusasphaeridium* which is erected herein to hold the two *Archaeperidinium* species discussed previously. The name proposed is *Asymmetropedinium* nom. nov. (see appendix), hence *Protoperidinium* (*Protoperidinium* sect. *Asymmetropedinium*) *punctulatum* for this species.

Cyst description. Spheroidal brown cyst made up of autophragm or two closely adpressed wall layers. Surface smooth, shagreenate, or slightly granulate. Paratabulation only revealed by archeopyle formation. Archeopyle intercalary formed by the loss of paraplate 2a. Operculum large, transversely elongate but asymmetrical. Cyst diameter ranges from 40·0 to 60 μm.

iii. Hexa. This group contains the following species that produce fossilizable cysts.

Protoperidinium (*Protoperidinium*) *conicoides* (Paulsen) Balech 1974

Text-fig. 18; Plate 38, figs. 1–3

Remarks. The epithecal tabulation of this species illustrates the nature of the ortho first apical plate and the hexa dorsal intercalary arrangement together with the symmetry. The cyst of this species has

---

EXPLANATION OF PLATE 40

All figures are illustrated at a magnification of × 500 and were photographed in plain transmitted light unless otherwise indicated.

Figs. 1–8. *Protoperidinium* cyst, *Lejeunia paratenella* Benedek. 1, low-focus dorsal view with attenuated hexa archeopyle. 2, high-focus dorsal view showing the paracingulum and nature of aciculate antapical horns. 3, ventral view with slightly displaced paracingulum, specimen MPK 2775. 4, dorsal view with archeopyle and denticulate cingular parasutures. 5, ditto in phase contrast, specimen MPK 2776. 6, dorsal view showing attenuated hexa archeopyle with operculum in place, Nomarski interference contrast. 7, ventral view, Nomarski interference contrast, specimen MPK 1247. 8, dorsal view with attenuated hexa archeopyle, Nomarski interference contrast, specimen MPK 1245.

Fig. 9. *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech, dorsal view with standard hexa archeopyle exhibiting slight apical tongue. Difference in archeopyle style between this and previous species is marked, specimen MPK 2777.

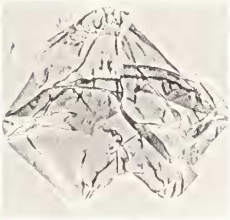
Figs. 10–12. *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *oblongum* (Aurivillius) Balech. 10, ventral view showing overall chordate morphology. 11, dorsal view with archeopyle truncating apex. 12, ditto, Nomarski interference contrast, specimen MPK 2778.

1

2

3

4



5

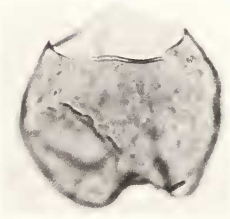
6

7

8

9

10

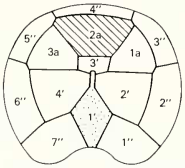


11

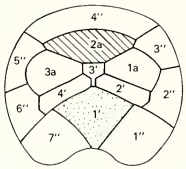
12

HARLAND, *Protoperidinium*

been described by Wall and Dale (1968), Reid (1977), and Harland (1977), and was originally placed in the cyst genus *Chytroeisphaeridia* as *C. simplicia* by Wall (1965). More recently it has been chosen as the type species for the cyst genus *Brigantedinium* Reid which has been validated by Harland and Reid (1980) in Harland *et al.* (1980). The cyst morphology is, like many other *Protoperidinium* cysts, a simple brown ball. This cyst has not been successfully incubated but the link between theca and cyst is almost certain (Wall and Dale 1968).



TEXT-FIG. 18. (*left*) Epithecal tabulation of *Protoperidinium* (*Protoperidinium*) *conicoides* (Paulsen) Balech (after Wall and Dale 1968).



TEXT-FIG. 19 (*right*). Epithecal tabulation of *Protoperidinium* (*Protoperidinium*) *conicum* (Gran) Balech (after Wall and Dale 1968).

Cyst description. A spherical brown cyst made up of autophragm which may be smooth, shagreenate, or loosely reticulate. May exhibit a slightly indented paracingular and parasulcal area, the latter possessing indications of the flagellar pores. Archeopyle formed by loss of a single intercalary paraplate (2a) of standard hexa shape which may show interesting detail around the margin (Pl. 38, fig. 1). This detail, especially, toward the apex, perhaps suggests the loss of more than just a single paraplate. Operculum free. Cyst diameters range from 30·0 to 50·0 μm.

This cyst can be distinguished from other similar cysts by the nature of its archeopyle (see earlier sections) but it is often difficult to recognize if the cysts are crushed.

Protoperidinium (*Protoperidinium*) *conicum* (Gran) Balech 1974

Text-fig. 19; Plate 39, figs. 1–3; Plate 42, figs. 1, 10

Remarks. The thecal epitabulation shows the main features of this group and is distinctly symmetrical. An interesting feature is, however, the almost rectangular shape of plates 2′ and 4′. The cysts of this species have been described by Wall and Dale (1968), Bradford (1975), Reid (1977), and Harland (1977). The cyst genus *Multispinula* Bradford has been applied to them although this is a junior synonym of *Selenopemphix* Benedek which was originally erected for cysts showing polar compression and an offset archeopyle (Stover and Evitt 1978). Bujak (1980) formally emended *Selenopemphix* to draw attention to this offset archeopyle and also to include spinose forms. Wall and Dale (1968) established the theca/cyst link by incubation studies.

Cyst description. Ovoidal to reniform cysts probably made up of two wall layers, the outer making up the solid aciculate processes. Cyst usually has a polar compression due to its general cyst morphology of low epicystal and hypocystal cones (see Wall and Dale 1968, pl. 2, figs. 4, 5). This compression may also have the effect of slightly rotating the epicyst to accentuate the offset archeopyle. Pl. 39, figs. 1–3 demonstrates the variable amount of offset of the archeopyle. The sulcal area is exhibited as an indentation in the ventral side of the ambitus and the paracingulum is displayed as a circumferential band. Processes are generally most common at the apex and circumference although they also occur all over the cyst. Archeopyle intercalary formed by the loss of paraplate 2a which exhibits a standard hexa shape and is asymmetrically placed. Operculum free. The offset archeopyle may indicate the utilization of an additional paraplate to the 2a in archeopyle formation. Cyst diameter 40·0 to 60·0 μm.

There is some confusion between these cysts and those of *P.* (*P.*) *nudum* that have a similar morphology but are smaller. Bradford (1975) and Reid (1977) argued that a continuous size gradation existed between the two such that only the one cyst species can be recognized in the absence of knowledge of the thecal morphology.

Protoperidinium (*Protoperidinium*) *leonis* (Pavillard) Balech 1974

Text-fig. 20; Plate 41, figs. 1–14; Plate 42, figs. 7, 9.

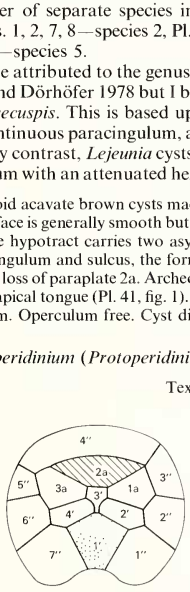
Remarks. The epithecal tabulation of this species indicates a possible assignment to the penta group and not to the hexa as Balech (1974) suggests, but Lebour (1925) has figured a specimen from Plymouth Sound with a clear hexa dorsal arrangement. Again some slight variation in the dorsal tabulation pattern is apparent. A symmetrical arrangement of plates on the epitheca is normal. The cysts of this species have been described by Evitt and Davidson (1964), Wall and Dale (1968), Bradford (1977), Reid (1977), and Harland (1977) using such generic taxa as *Lejeunia* Gerlach, *Trinovantedinium* Reid and *Quinquecuspis* Harland (see Harland 1977 for some synonymies). Wall and Dale (1968) established the theca/cyst link by incubation but had difficulty in distinguishing *P. leonis* from such species as *P. marielebourae* (Paulsen) and *P. obtusum* (Karsten). The range of cyst morphologies place within *P.* (*P.*) *leonis* reinforces the need for further study as it is perfectly possible that there are a number of separate species involved, including those represented in Pl. 40, fig. 9—species 1, Pl. 41, figs. 1, 2, 7, 8—species 2, Pl. 41, figs. 3–6—species 3, Pl. 41, figs. 9, 10—species 4 and Pl. 41, figs. 11–14—species 5.

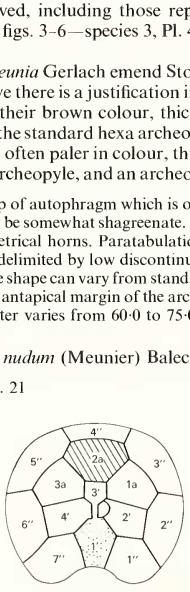
All these forms can be attributed to the genus *Lejeunia* Gerlach emend Stover and Evitt 1978 now *Lejeunecysta* Artzner and Dörhöfer 1978 but I believe there is a justification in keeping them within a separate taxon, *Quinquecuspis*. This is based upon their brown colour, thick wall, deeply indented parasulcus, often discontinuous paracingulum, and the standard hexa archeopyle, and an archeopyle index of *c.* 0·35–0·45. By contrast, *Lejeunia* cysts are often paler in colour, thin walled, have a planar continuous paracingulum with an attenuated hexa archeopyle, and an archeopyle index of *c.* 0·2–0·3.

Cyst description. Peridinioid acavate brown cysts made up of autophragm which is often thickened at the apex and antapex. The cyst surface is generally smooth but may be somewhat shagreenate. Epitract may be conical or have shoulders, whilst the hypotract carries two asymmetrical horns. Paratabulation may be represented by distinctly indented paracingulum and sulcus, the former delimited by low discontinuous or continuous ridges. Archeopyle intercalary by loss of paraplate 2a. Archeopyle shape can vary from standard hexa (Pl. 41, figs. 3, 14) to standard hexa with an apical tongue (Pl. 41, fig. 1). The antapical margin of the archeopyle is often at, or very close to, the paracingulum. Operculum free. Cyst diameter varies from 60·0 to 75·0 μm.

Protoperidinium (*Protoperidinium*) *nudum* (Meunier) Balech 1974

Text-fig. 21





TEXT-FIG. 20 (*left*). Eptithecal tabulation of *Protoperidinium* (*Protoperidinium*) *leonis* (Pavillard) Balech (after Wall and Dale 1968).

TEXT-FIG. 21 (*right*). Epithecal tabulation of *Protoperidinium* (*Protoperidinium*) *nudum* (Meunier) Balech (after Wall and Dale 1968).

Remarks. The epithecal tabulation pattern shows all the usual features of this group; the ortho first apical and the hexa dorsal intercalary arrangement. The cyst has been described by Wall and Dale (1968) as being similar to those of *P.* (*P.*) *conicum* but smaller (31.0 μm, excluding spines as compared to 50.0 μm for *P.* (*P.*) *conicum*), and possessing relatively longer spines with conical bases. The archeopyle is formed by the displacement of the dorsal intercalary paraplate (2a). The attached operculum carries two spines. The confusion in distinguishing this cyst from those of *conicum* in palynological preparations has already been noted. Wall and Dale (1968) incubated two thecae from cysts but some doubt in identification of the thecae is apparent from their ?*nudum* designation.

Protoperidinium (*Protoperidinium*) *pentagonum* (Gran) Balech 1974

Text-fig. 22; Plate 39, figs. 7–11; Plate 42, fig. 8

Remarks. This species fits well into this group by virtue of its epithecal tabulation whereas its cyst, described by Wall and Dale (1968), Bradford (1977), Reid (1977), and Harland (1977), is somewhat different from those described above. It has in fact been described under the names *Lejeunia applanata* by Bradford (1977) and *Trinovantedinium capitatum* by Reid (1977) and Harland (1977).

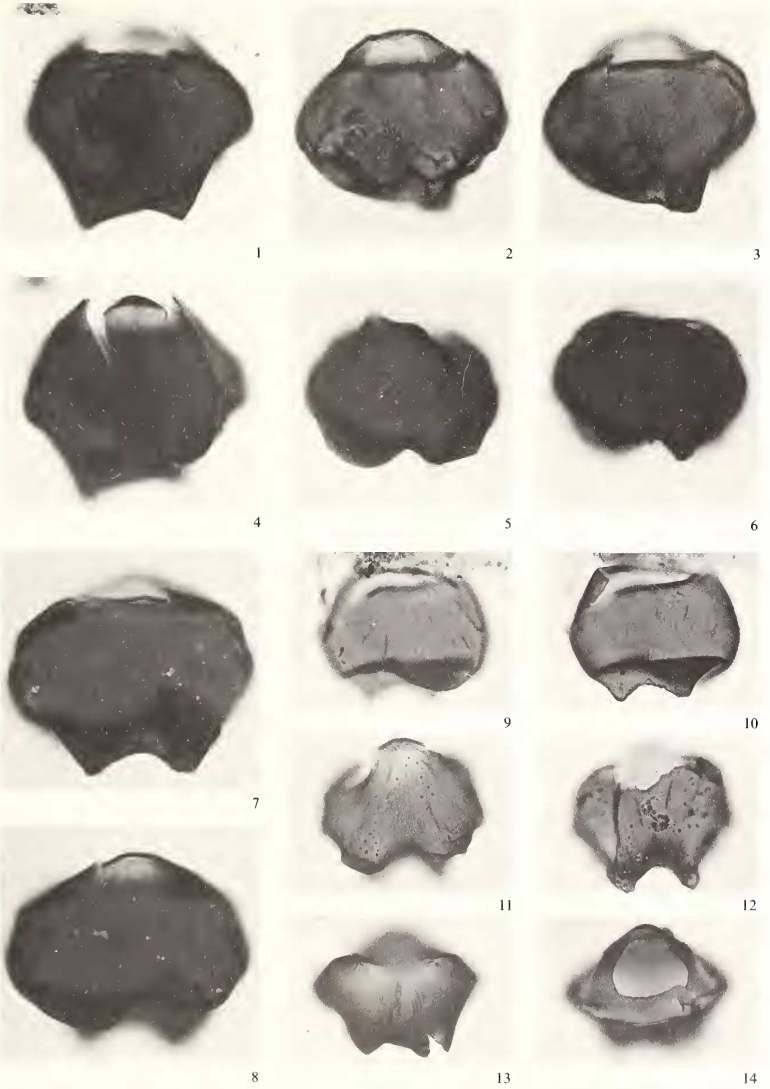
This cyst is quite distinct from others described within this group by virtue of its hyaline wall, possession of short sutural and intratabular spines, and a broad hexa archeopyle. The cyst of *P.* (*P.*) *pentagonum* was chosen by Reid (1977) as the type for his genus *Trinovantedinium*. This genus was used to accommodate other cysts, especially those having thick brown walls, a peridinioid outline, and standard hexa archeopyle. I prefer to restrict the genus *Trinovantedinium* to include the cyst of *P.* (*P.*) *pentagonum* and any similar forms (see Wall and Dale 1968, pl. 2, figs. 9–10 and 11–12 and Bradford 1977), but not to include brown cysts with standard hexa archeopyles. The cyst *Sumatradinium hispidum* (Drugg) Lentin and Williams could be related. Wall and Dale (1968) incubated a cyst to establish the cyst/theca relationship for *P.* (*P.*) *pentagonum*. However, other similar cysts produced thecae with minor differences such that a number of separate species or varieties may be involved.

Cyst description. Pentagonal peridinioid cyst made up of autophragm, epicyst with apical boss, and sometimes shoulders. Hypocyst has two slightly asymmetrical antapical horns or bulges. Paratabulation not easily recognized except for the planar non-indented paracingulum marked by sutural line of processes, the deeply indented parasulcus, and the pattern of intratabular processes defining paraplate areas. Processes are short, rigid with hollow bulbous bases, fine, aciculate with bifid, capitate, or infundibular solid tips. Processes are both sutural and intratabular but their dispositions are not sufficiently clear to reveal the paratabulation. Archeopyle intercalary formed by the loss of 2a paraplate, operculum free, archeopyle is a broad hexa style (Pl. 39, fig. 10). Cyst maximum length ranges from 65·0 to 70·0 μm.

EXPLANATION OF PLATE 41

All figures are illustrated at a magnification of $\times$ 500 and were photographed in plain transmitted light unless otherwise indicated.

Figs. 1–14. *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech. 1, dorsal view with archeopyle and operculum showing a clear apical tongue. 2, ventral view with deeply indented parasulcus and somewhat discontinuous paracingulum, specimen MPK 1230. 3, ventral view with standard hexa archeopyle, apical margin by transparency. 4, dorsal view, specimen MPK 2779. 5, ventral view with deeply indented parasulcus and discontinuous paracingulum. 6, dorsal view, specimen MPK 2780. 7, dorsal view showing posterior archeopyle margin almost affecting the paracingulum. 8, ventral view, specimen MPK 2781. 9, ventral view. 10, dorsal view, specimen MPK 2782. 11, ventral view with deep parasulcus and discontinuous paracingulum. 12, dorsal view, specimen MPK 2783. 13, ventral view with two flagellar parapores. 14, dorsal view showing standard hexa archeopyle with no apical tongue, specimen MPK 2784.



HARLAND, *Protoperidinium*

Protoperidinium (*Protoperidinium*) *subinerme* (Paulsen) Loeblich, III, 1969

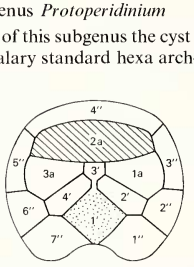
Text-fig. 23; Plate 39, fig. 6

Remarks. The thecal tabulation reveals the ortho first apical plate and the dorsal epithecal style. The cyst of this species has been described by Wall and Dale (1968) as being characterized by a relatively wide and deeply indented cingulum. The cyst illustrated here (Pl. 39, fig. 6) is believed to be attributable to *P.* (*P.*) *subinerme*. Wall and Dale (1968) established the theca/cyst relationship of this species although they recognized that the resultant theca from incubation was more elongate in the polar direction than other thecae of this species.

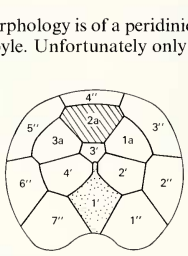
Cyst description. Ovoidal to reniform cysts, usually with a polar compression due to the low cone morphology of the epi- and hypocyst. Marked paracingular zone characterized by a broad circumferential band. Cyst smooth, light brown in colour, and possessing an offset standard hexa intercalary archeopyle formed by the displacement of ?2a paraplate. Operculum may be attached. Cyst diameter ranges from 45·0 to 60·0 μm.

Discussion of the subgenus *Protoperidinium*

Within the para species of this subgenus the cyst morphology is of a peridinioid form with a reduced hypocyst and an intercalary standard hexa archeopyle. Unfortunately only one cyst type is known



TEXT-FIG. 22 (*left*). Epithecal tabulation of *Protoperidinium* (*Protoperidinium*) *pentagonum* (Gran) Balech (after Wall and Dale 1968).



TEXT-FIG. 23 (*right*). Epithecal tabulation of *Protoperidinium* (*Protoperidinium*) *subinerme* (Paulsen) Loeblich, III (after Wall and Dale 1968).

EXPLANATION OF PLATE 42

All figures, except the stereoscan photomicrographs, are illustrated at a magnification of × 500 and were photographed in Nomarski interference contrast.

Fig. 1. *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *conicum* (Gran) Balech, specimen MPK 2949. A small specimen at the lower end of the size range that could be confused with *P.* (*P.* sect. *Selenopemphix*) *nudum* (Meunier) Balech.

Fig. 2. Indet. *Protoperidinium* cyst, specimen MPK 2950, with a well developed zigzag split archeopyle.

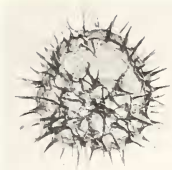
Figs. 3–6. *Protoperidinium* (*Protoperidinium* sect. *Asymmetropedinium*) *punctulatum* (Paulsen) Balech, specimen MPK 2951, 2952 and 2953) respectively. Specimens showing the over-all cyst morphology and nature of operculum, particularly its asymmetrical morphology.

Fig. 7. *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech, specimen MPK 2954 showing cyst morphology and archeopyle, together with a continuous paracingulum, × *c.* 1000.

Fig. 8. *Protoperidinium* (*Protoperidinium* sect. *Trinovantedinium*) *pentagonum* (Gran) Balech, specimen MPK 2956, showing cyst morphology and the broad hexa archeopyle, × *c.* 1000.

Fig. 9. Indet. *Protoperidinium* cyst, specimen MPK 2957. Could be part of the cyst variation as currently attributed to *P.* (*P.* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech, × *c.* 1000.

Fig. 10. *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *conicum* (Gran) Balech, specimen MPK 2958, showing over-all cyst morphology, × *c.* 1000.



1

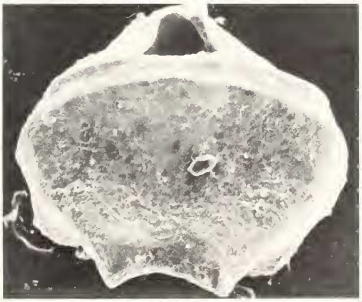
2

3

4

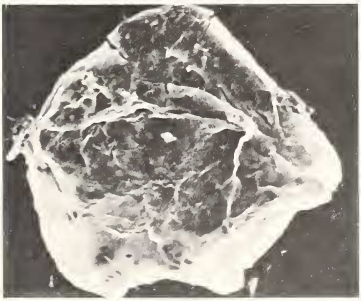
5

6

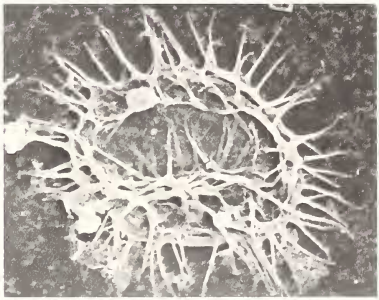


7

8



9



10

HARLAND, *Protoperidinium*

from this group at the present time. The designation *Protoperidinium* (*Protoperidinium* sect. *Protoperidinium*) may be used for thecae with a para first apical and hexa dorsal intercalary arrangement and for peridinioid cysts with reduced hypocysts. However, it must be admitted that the type species does not appear to have fossilizable cysts.

In the ortho species we have most of the living cyst species including, in the quadra subsection, the chordate cysts, with or without spines and having an archeopyle that truncates the apex, i.e. the species *P.* (*P.*) *claudicans* and *P.* (*P.*) *oblongum* respectively. The designation *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) can be used for these ortho, quadra species.

Amongst the ortho penta species only the cyst of *P.* (*P.*) *punctulatum* is known, and like so many *Protoperidinium* cysts it is a brown sphere. It is, however, characterized by its archeopyle which is transversely elongate and asymmetrical. The name *Asymmetropedinium* is proposed at section level to accommodate this species.

In the ortho hexa species a fourfold division based upon cyst morphology is possible. The thecal tabulation does not in itself support this division but perhaps other factors need to be considered. The first division is represented by *P.* (*P.*) *conicoides* which has a spherical brown cyst with a standard hexa archeopyle; the second by *P.* (*P.*) *conicum*, *P.* (*P.*) *nudum*, and *P.* (*P.*) *subinerme* that have cysts commonly showing polar compression because of the low conate shape of the epi- and hypocyst, and an offset standard hexa archeopyle. A third type represented by *P.* (*P.*) *leonis* contains brown peridinioid cysts with standard hexa archeopyles and finally the fourth is characterized by *P.* (*P.*) *pentagonum* with a hyaline peridinioid cyst with a broad hexa archeopyle. The names *Brigantedinium* Reid, *Selenopemphix* Benedek, *Quinquecuspis* Harland, and *Trinovantedinium* Reid respectively are used here to designate these dinoflagellates at section level and are names that were first established in the palaeontological literature.

Unattributed *?Protoperidinium* cysts

Remarks. There are many *?Protoperidinium* cysts described in the literature that have been observed in palynological assemblages of Recent sediments, but whose attribution to the thecate stage is unknown. A number of such forms are illustrated and commented upon here. The first (Pl. 38, figs. 10–12, and Pl. 42, fig. 2) is in essence a brown spherical cyst that opens by means of a zigzag split. Reid (1972) described such cysts from intertidal sediments around the British coast. It is interesting to note that the brown spherical morphology is again apparent, but that the archeopyle morphology is sufficiently different to differentiate these cysts from the other forms described earlier. It is, however, quite possible that these cysts are from glenodiniacean dinoflagellates such as *Diplopsalis* (see Wall and Dale 1986, pl. 4, fig. 20).

A second type, that has been described under the name of *Xandarodinium xanthum* Reid 1977, is illustrated on Pl. 39, figs. 4–5. This cyst has a unique morphology with hollow processes carrying distal furcate and bifid tips. Reid (1977) describes these cysts as having a possible single paraplate intercalary archeopyle, but an archeopyle has not been seen by me. The morphology in regard to the ovoidal/reniform ambitus suggests a polar compression and hints at an attribution to sect. *Selenopemphix*, but confirmation and details of archeopyle formation must await further study. *Artemisiocysta cladodichotoma* Benedek may be related to the cyst form described here. This cyst might be a representative of a gymnodinialean dinoflagellate (see Wall and Dale 1968, pl. 4, fig. 29).

The final type (Pl. 40, figs. 1–8) has been referred to as *Lejeunia paratenella* Benedek 1972 by Harland (1977) and *Trinovantedinium olivum* Reid 1977 by Reid (1977). It is characterized by its peridinioid outline, pale brown colour, thickened apex and antapex, the latter often developed into acicular horns, planar paracingulum delimited by denticulate sutures, and an attenuated hexa archeopyle (Lentin and Williams 1975). This cyst differs, therefore, from those referred to as *Quinquecuspis*, and I prefer to see it accommodated in *Lejeunecysta* Artzner and Dörhöfer 1978. Lentin and Williams (1975) have attributed a standard hexa archeopyle to *Lejeunecysta* (as *Lejeunia*), but the nature of the archeopyle in the type species has not been clearly demonstrated. The specimen figured by Benedek (1972) does, however, appear to have a standard hexa archeopyle which may

indicate that *Lejeunecysta* is a senior of *Quinquecuspis* and that a new name needs to be erected for these cysts. Until the thecate form is identified further speculation is unwarranted.

GENERAL DISCUSSION

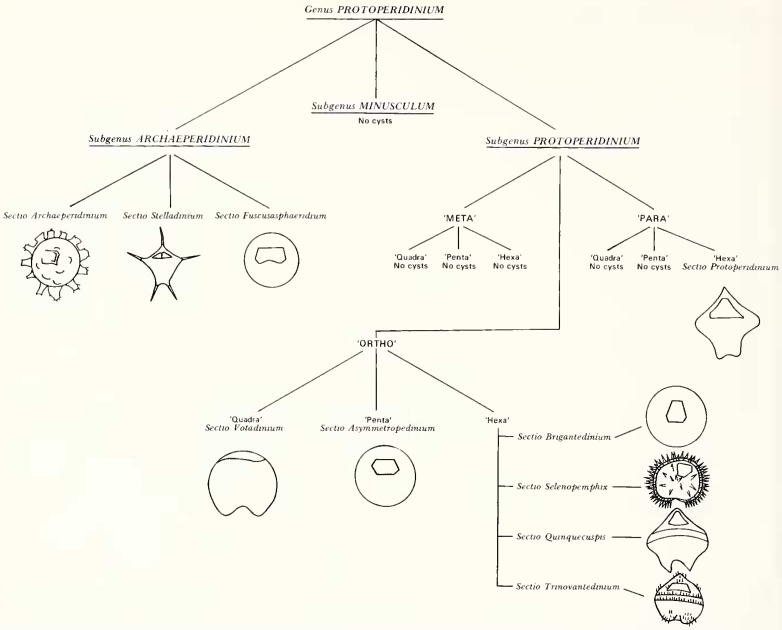
A taxonomic system capable of amalgamating both cyst and thecal data must be one of the aims of dinoflagellate research and would inevitably lead to a rationalization of much of our fossil data. The exercise, outlined above, tests that possibility and shows this, or a similar system, is practical. It is clear that both the major and minor divisions of the genus *Protoperidinium* Bergh are largely upheld by differing cyst morphologies (text-fig. 24). The genus is basically characterized by cysts of spherical to peridinioid shape, possessing an intercalary archeopyle. The subgenus *Archaeperidinium* is characterized by such unique cysts as those of *P.* (*A.*) *minutum*, *P.* (*A.*) *compressum*, and simple brown spherical cysts distinguished by broad hexa, transversely elongate, symmetrical archeopyles. Cyst morphology can also be used to further subdivide the subgenus at section level. These subdivisions need, however, further testing in relation to total dinoflagellate morphology.

Similarly the subdivisions of the subgenus *Protoperidinium* based upon thecal morphology appear to be largely substantiated by differences in cyst construction. The para species may have cysts with reduced hypocysts and no paracingulum (but the evidence is based upon one species only). The different divisions of the ortho forms have the following morphologies; the quadra cysts are chordate in shape with an archeopyle that is basically intercalary but truncates the apex and may involve additional paraplates; the penta cysts are brown and spherical, with a broad hexa archeopyle that is asymmetrical; and the hexa cysts are both spherical and peridinioid, with standard or broad hexa archeopyles. In this last case the cyst morphologies may serve to further subdivide the group.

Dale (1978) has pointed out that dinoflagellate cysts are often non-conservative, with large differences in cyst morphology being reflected by small 'minor' differences in thecae. This is supported by the present study; indeed in the ortho hexa cysts large differences in cyst morphology are seemingly not reflected in thecal morphology at all. In my view, major and minor differences in morphology are relative terms. What should be remembered is that the genetic information is common to both stages of the life cycle, and that all morphological differences must be critically evaluated. Dinoflagellate taxonomy should be based upon the holomorph where possible or on as much information as is available such that a common taxonomy can evolve. In this way it is necessary to evaluate both the cyst-based taxonomy, often 'overclassified' and the thecate-based taxonomy, often 'underclassified' (Dale 1978), in order to arrive at the best amalgamation. Whilst agreeing with Dale (1978) that new cyst-based nomenclature should not be created to artificially maintain the cyst-based taxonomy, much useful information can be derived from good taxonomic work based upon cysts, thecae, or on both.

From a review of this nature the major difference between the thecal-based taxonomy and the cyst-based system is one of hierarchy (see text-fig. 24). The palynologist would regard his cyst taxa as separate genera whereas the phycologist might be prepared to accept them at section level. Once this hierarchical difference is recognized, the conflict between the two systems largely vanishes and both theca and cyst data can point to areas where further study is needed to help resolve or enlarge upon taxonomic decisions. In addition, it should assist the palynologist to view his fossil taxa in a better perspective. It is clear, however, that the species is the common denominator, is constant, and should be the basis of all our mutual research.

This study has also highlighted the 'variation' in thecal and cyst morphologies, especially in the ortho quadra species, which appear to have both quadra and penta dorsal configurations as in *P.* (*P.*) *claudicans*, the ortho hexa species such as *P.* (*P.*) *leonis* with both penta and hexa configurations, and the ortho penta species such as *P.* (*P.*) *punctulatum* that have both penta and hexa dorsal epithecal patterns. In the ortho quadra group the data also suggest variation in cyst morphologies, from chordate cysts with archeopyles truncating the apex to cysts with a peridinioid shape and standard hexa archeopyles. Recent studies have tended to show that the dorsal epithecal and epicystal pattern



TEXT-FIG. 24. Recent and Quaternary *Protoperidinium* cyst types and their respective positions in the taxonomic subdivision of the genus.

is of considerable importance in dinoflagellate organization as both the keystone plate and overlap system, together with archeopyle position, all relate to that pattern, and suggest a common genetic control.

Some of the 'variation' discussed may in fact be more artificial than real, because much of it is inextricably linked to taxonomic difficulties. The examples of *P.* (*P.*) *oblongum* and *P.* (*P.*) *leonis* are cases in point. Much of these difficulties will need detailed research on both thecal and cyst morphologies, together with population studies, before any satisfactory conclusions can be reached.

There is a range of cyst types associated with a single living genus, i.e. from simple brown spheres to peridinoid and quite complex stellate morphologies. The cyst types are, however, dominated by two cyst morphologies—the simple brown spheres and the peridinoid cysts. the intercalary archeopyle is a common factor throughout, although its shape, style, and involvement of adjacent paraplates is different in the separate groups. The occurrence of the simple brown spherical cyst morphology in the subgenera *Archaeperidinium* and *Protoperidinium* (and in both ortho penta and ortho hexa groups) may be cited as a good example of the development of a common cyst form by different dinoflagellates (homoeomorphy). Indeed this morphology is also seen in cysts of unknown affinity (see Pl. 38, figs. 10–12) and in the glenodiniacean dinoflagellates (Reid 1977). There is difficulty in recognizing species among these brown spheres because of a usual lack of well-preserved and well-orientated specimens. In addition, brown peridinioid cysts also occur in more than one dinoflagellate group.

It is interesting to observe the lack of correspondence between some dorsal epithecal tabulations and the partial paratabulations revealed by archeopyle formation. In particular, the stellate cyst of *P.* (*A.*) *compressum* appears to have a symmetrically placed type 2I archeopyle but not a symmetrical dorsal epithecal tabulation pattern. Similarly *P.* (*P.*) *conicum*, *P.* (*P.*) *nudum*, and *P.* (*P.*) *subinerme* have symmetrically placed 2a thecal plates, but offset type I archeopyles. Although the over-all genetic control is apparent there does not seem to be a strict template mechanism. Whether or not additional paraplates are involved in these cases in archeopyle formation, there is an obvious need for caution. The mechanism and control of archeopyle formation is a fascinating question and is clearly more complex than at first appears.

Unfortunately there are still a number of cysts, described in the literature, of possible *Protoperidinium* affinity, whose 'parental' thecae are not known. One of these is the cyst referred to as *Lejeunia paratenella* Benedek by Harland (1977). It would be of special interest to know the thecal affinity of *L. paratenella* in order to compare it with other *Protoperidinium* species known to produce *Quinquecuspis* type cysts. This should serve to help in understanding the nature of *Lejeunecysta*/*Quinquecuspis* species in the fossil record.

Other fossil cysts may be underrepresented within this scheme because of their susceptibility to oxidation in nature, in the palynological preparation technique, and to treatment with strong acids (Dale 1976; Reid 1972). It is apparent from Lentin and Williams (1975) that the fossil record of the genus *Protoperidinium* includes only those cysts attributable to the subgenus *Protoperidinium*, including ortho forms, such as the fossil genera *Rhombodinium* Gocht and *Wetzeliella* Eisenack, which have a geological record from the Palaeocene, and ortho forms such as *Alterbia* Lentin and Williams and *Deflandrea* Eisenack, with records from at least the Albian. Other peridiniacean cysts with more complex compound archeopyles are not represented here. The cysts portrayed within the sections *Selenopemphix* and *Quinquecuspis*/*Lejeunecysta* have fossil records at least as far back as the Late Eocene and Late Cretaceous respectively.

CONCLUSIONS

This study should have demonstrated the feasibility of combining cyst and thecate morphological data into a sensible taxonomic scheme which might be of some application to both Quaternary and some Tertiary peridiniacean dinoflagellates. It is, of course, not complete, because much more thecal data are needed before a fully comprehensive taxonomy can be attempted. I hope it does suggest a possible way forward and one that could be equally applied to gonyaulacacean, glenodiniacean, ceratiacean, or pyrophacacaean dinoflagellates where and when sufficient evidence is available. Notable points of interest have been the morphological range of cysts from a single living genus, and the hierarchical difference between the sections erected herein and what would be undoubtedly regarded as separate genera by palynologists. The species concept does, however, appear to be a mutually acceptable base.

Acknowledgements. The author would like to acknowledge the various discussions with Dr J. P. Bujak, Geological Survey of Canada, Mr B. Dale, University of Oslo, Dr P. C. Reid, Institute for Marine Environment Research, Professor W. A. S. Sarjeant, University of Saskatchewan, and Dr L. E. Stover, Exxon Production Research, on the nature and classification of *Protoperidinium* cysts. However, the views expressed herein are solely his responsibility. I thank Barrie Dale, and Drs Evitt and Reid for their critical reading. This paper was presented at the V International Palynological Conference in Cambridge, June 1980. Thanks are also due to Mrs Jane Sharp for her excellent preparations and single grain mounting, to Mrs Sue Crook for her draughting skills, and to Mrs Margaret Metcalfe for her typing. Latin translation of the various diagnoses are by Mr John A. Rooney. This paper is published with permission from the Director, Institute of Geological Sciences (N.E.R.C.).

REFERENCES

ARTZNER, D. G. and DÖRHÖFER, G. 1978. Taxonomic note: *Lejeunecysta* nom. nov. pro. *Lejeunia* Gerlach 1961 emend. Lentin and Williams 1976—dinoflagellate cyst genus. *Can. J. Bot.* **56,** 1381–1382.

BALECH, E. 1974. El genero 'Protoperidinium' Bergh, 1881 ('Peridinium' Ehrenberg, 1831, partim.). *Rev. Mus. Cienc. natur., Hidrobiol.* **4,** 1–79.

BENEDEK, P. N. 1972. Phytoplanktonten aus dem Mittel- und Oberologozän von Tönisberg (Niederrheingebeit). *Palaeontographica*, Abt. B, **137,** 1–71.

BRADFORD, M. R. 1975. New dinoflagellate cyst genera from the recent sediments of the Persian Gulf. *Can. J. Bot.* **53,** 3064–3074.

—— 1977. New species attributable to the dinoflagellate cyst genus *Lejeunia* Gerlach, 1961 *emend.* Lentin and Williams 1975. *Grana*, **16,** 45–59.

BUJAK, J. P. 1980. Dinoflagellate cysts and acritarchs from the Eocene Barton Beds of southern England. *In* BUJAK, J. P., DOWNIE, C., EATON, G. L. and WILLIAMS, G. L. Dinoflagellate cysts and acritarchs from the Eocene of southern England. *Palaeontology, Spec. Pap.*, **24,** 36–91.

DALE, B. 1976. Cyst formation, sedimentation, and preservation: factors affecting dinoflagellate assemblages in Recent sediments from Trondheimsfjord, Norway. *Rev. Palaeobot. Palynol.* **22,** 39–60.

—— 1978. Acritarchous cysts of *Peridinium faeroense* Paulsen: implications for dinoflagellate systematics. *Palynology*, **2,** 187–193.

DÖRHÖFER, G. and DAVIES, E. H. 1980. Evolution of archeopyle and tabulation in Rhaetogonyaulacinean dinoflagellate cysts. *Life Sciences Miscell. Publ., Royal Ontario Museum*, 1–91.

DÜRR, G. and NETZEL, H. 1974. The fine structure of the cell surface in *Gonyaulax polyedra* (Dinoflagellata). *Cell Tiss. Res.* **150,** 21–41.

EDWARDS, L. E. and BEBOUT, J. W. 1981. Emendation of *Phthanoperidinium* Drugg and Loeblich 1967, and a description of *P. brooksii* sp. nov. from the Eocene of the mid-Atlantic outer continental shelf. *Palynology*, **5,** 29–41.

ENRENBERG, C. G. 1832 [separate 1830]. Beiträge zur Kenntniss der Infusorien und ihrer geographischen Verbrietung besonders in Sibirien. *Abh. preuss. Akad. Wiss.* 1830, 1–88.

EVITT, W. R. and DAVIDSON, S. E. 1964. Dinoflagellate Studies I. Dinoflagellate cysts and thecae. *Stanford Univ. Publs., Geol. Sci.* **10 (1),** 1–12.

GOCHT, H. and NETZEL, H. 1974. Rasterelektronenmikroskipische Untersuchungen am Panzer von *Peridinium* (Dinoflagellata). *Arch. Protistenk.* **116,** 381–410.

—— —— 1976. Reliefstrukturen des Kreide—Dinoflagellaten *Palaeoperidinium pyrophorum* (Ehr.) in Vergleich mit Panzer-Merkmalen rezenter *Peridinium*-Arten. *Neues Jb. Geol. Paläont., Abh.* **153,** 380–413.

GRAHAM, H. W. 1942. Studies in the morphology, taxonomy, and ecology of the Peridiniales. *Carnegie Institution of Washington*, **542,** 1–129.

HARLAND, R. 1977. Recent and Late Quaternary (Flandrian and Devensian) dinoflagellate cysts from marine continental shelf sediments around the British Isles. *Palaeontographica*, Abt. B, **164,** 87–127.

—— REID, P. C., DOBELL, P. and NORRIS, G. 1980. Recent and sub-Recent dinoflagellate cysts from the Beaufort Sea, Canadian Arctic. *Grana*, **19,** 211–225.

JÖRGENSEN, E. (1912) 1913. Bericht über die von der schwedischen Hydrographisch—Biologischen Kommission in den schwedischen Gewässern in den Jahren 1909–1910 eingesammelten Planktonproben. *Svenska hydrogr.—biol. komm. Skr.* **4,** 1–20.

LEBOUR, M. V. 1925. The dinoflagellates of northern seas. *Mar. Biol. Assoc. U.K.*, Plymouth, 1–250.

LENTIN, J. K. and WILLIAMS, G. L. 1975. A monograph of fossil peridinioid dinoflagellate cysts. *Bedford Inst. of Oceanogr. Rept.* BI-R-75-16, 1–237.

PAULSEN, O. 1931. Études sur le microplankton de la Mer d'Alboran. *Trab. Inst. esp Oceanogr.* **4,** 5–108.

REID, P. C. 1972. The distribution of dinoflagellate cysts, pollen and spores in Recent marine sediments from the coast of the British Isles. Unpubl. Ph.D. thesis, Univ. of Sheffield, 1–273.

—— 1977. Peridiniacean and glenodiniacean dinoflagellate cysts from the British Isles. *Nova. Hedwigia*, **24,** 429–463.

—— and HARLAND, R. 1977. Studies of Quaternary dinoflagellate cysts from the North Atlantic. *Am. Ass. stratigr. Palynol., Contr. Ser.* **5A,** 147–169.

STAFLEU, F. A. *et al.* 1978. *International Code of Botanical Nomenclature*. Bohn, Scheltema & Holkema, Utricht, 1–457.

STOVER, L. E. and EVITT, W. R. 1978. Analyses of pre-Pleistocene organic-walled dinoflagellates. *Stanford Univ. Publs. Geol Sci.* **15,** 1–298.

WALL, D. 1965. Modern hystrichospheres and dinoflagellate cysts from the Woods Hole region. *Grana palynol.* **6,** 297–314.

WALL and DALE, 1968. Modern dinoflagellate cysts and evolution of the Peridiniales. *Micropaleontology*, **14**, 265–304.

REX HARLAND
Institute of Geological Sciences
Ring Road Halton
Leeds LS15 8TQ

Typescript received 12 January 1981
Revised typescript received 29 March 1981

APPENDIX

The appendix is used here to indicate new names, and names whose status has been altered. The order adopted follows that presented in the main text.

Subgenus *Archaeperidinium* (Jörgensen) Balech 1974

Section *Archaeperidinium* Jörgensen stat. nov.

Type species. Protoperidinium (*Archaeperidinium* sect. *Archaeperidinium*) *minutum* (Kofoid) Loeblich, III, 1969

Remarks. This name has been used at generic level by Jörgensen (1913), at sub-generic level by Balech (1974), and here is used at section level as one of the sections of the subgenus *Archaeperidinium*. It is characterized by cysts with unique process structure and a symmetrical epithecal tabulation pattern.

Section *Stelladinium* Bradford 1975 ex Harland and Reid 1980 stat. nov.

Type species. Stelladinium reidii Bradford 1975 ≡ *Protoperidinium* (*Archaeperidinium* sect. *Stelladinium*) cf. *compressum* (Abé) Balech 1974.

Remarks. This name, originally erected as a genus, is altered in status to become a section of the subgenus *Archaeperidinium*. The type species *reidii* is based upon a cyst holotype and not a thecate form but the parent must be a species similar to *P. compressum*. It is characterized by stellate cysts and an asymmetrical thecal tabulation.

Section *Fuscusasphaeridium* nom. nov.

Derivation of name. Latin: *fuscus*, brown, *sphaera*, ball.

Diagnosis. Spherical to spheroidal brown cyst of autophragm with a laterally elongate, symmetrical, archeopyle formed by the loss of a single intercalary paraplate (2a). Margin of archeopyle often shows its configuration with paraplates 3′, 4′, 1a, and 6″. Operculum free.

Cista autophragmatis aurea quae forman habet sphericalem vel spheroidalem et latus elongatum, symmetricalis est. Archaeopyla facta est uno paraplato intercalari amisso (? 2a). Margo archaeopylae saepe configurationem suam ostendit cum paraplatis 3′, 4′ 1a et 6″. Operculem liberum est.

Type species. Protoperidinium (*Archaeperidinium* sect. *Fuscusasphaeridium*) *avellana* (Meunier) Balech 1974 ≡ *Protoperidinium avellana* Meunier 1919, pp. 56, pl. 18, figs. 37–41. Recent.

Remarks. The new section erected here accommodates those dinoflagellates possessing brown spherical cysts with symmetrical, transversely elongate archeopyles and with slightly asymmetric dorsal epithecal tabulations.

Subgenus *Protoperidinium* (Bergh) Balech 1974

Section *Protoperidinium* Bergh 1881 stat. nov.

Type species. Protoperidinium (*Protoperidinium* sect. *Protoperidinium*) *pellucidum* Bergh 1881.